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# THE ANOLES (SAURIA, IGUANIDAE) OF THE GUADELOUPÉEN ARCHIPELAGO

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# No. 11 — *The Anoles (Sauria, Iguanidae) of the Guadeloupéen Archipelago*[1]

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## INTRODUCTION

The archipelago which lies between Dominica and Montserrat in the northern portion of the Lesser Antillean chain represents both a political and a geographical unit. Part of the French West Indies, and of the Republic of France, it is comprised of four large islands — La Guadeloupe (often, though erroneously, called "Basse-Terre" for its capital city) Grande Terre, La Désirade, and Marie Galante — and a number of smaller islands: Ilet-à-Kahouanne, Ilet-à-Fajou, Ilet-à-Cochons (ou Gouvernement), plus two island groups, Les Iles da la Petite Terre, and Les Iles des Saintes. Taken together, these islands may be referred to as the Guadeloupéen archipelago, named for La Guadeloupe, the largest of them.

The Guadeloupéen archipelago is not a geological unit. La Guadeloupe itself, about 25 miles long and 15 miles wide, contains a central spine of mountains that reach nearly 5,000 feet (1,467 meters) above sea level. Many of these mountains are still actively volcanic, and attest to the process which has built this land mass. Grande Terre, on the other hand, though nearly as large in area, is low, rather flat throughout, and comprised of oceanic limestone overlying an ancient volcanic base. Following Davis (1926), La Guadeloupe may be taken as representative of the "first cycle" islands of the Lesser Antilles, and Grande Terre as representative of the "second cycle" islands.

The first cycle islands are composed of volcanic rock and have never been submerged and recapped with limestone. Along with La Guadeloupe, Les Iles des Saintes and Ilet-à-Kahouanne are members of this group; Les Iles des Saintes and Ilet-à-Kahouanne are, however, no longer actively volcanic, and are the severely eroded remnants of once larger land areas. The latter islands may be considered as among the oldest remaining in the first cycle.

The second cycle islands, though of volcanic origin, have subsequently been submerged and capped with limestone. Grande Terre, Ilet-à-Cochons, La Désirade, Les Iles de la Petite Terre, and Marie Galante, taken together, constitute the southernmost

[1] The Anoles of the Eastern Caribbean. Part VII.

limit of the second cycle in the Lesser Antilles. There is no information available to me on their relative ages.

Ilet-à-Fajou is in reality an extensive mangrove swamp. It lies in the shallow Grande Cul-de-Sac Marin, and appears to be a product of the predominant northeast wind: a collection of detritus banked up along a strip of coral reef. Its northern edge is a few meters above sea level, and is, even during the rainy season when I was there, a dusty bit of barren desert. Squeezed between this small area of desert and the sea is a narrow band of scrub and thornbush where the anoles of Ilet-à-Fajou are to be found.

In general, *Anolis* are found throughout the archipelago wherever more than herb-stage vegetation occurs; they are not, however, apparently found on the highest peaks of La Guadeloupe. In the last revision of Lesser Antillean *Anolis*, by Underwood (1959), the five named taxa of the Guadeloupéen archipelago were reviewed; *marmoratus*, *ferreus*, and *speciosus* (with two subspecies) were considered distinct at the species level from other *Anolis* of the *bimaculatus* species group. A fifth form, *alliaceus*, was considered to be a subspecies of *bimaculatus* itself (the type locality of *bimaculatus* is St. Eustatius, separated by four islands on three banks and several hundred miles from the Guadeloupéen archipelago), and a sixth form, the Désirade anole, was granted specific status, but not described and named. In his discussion of *alliaceus*, Underwood (p. 200) notes that Williams regarded that form, *sensu* Underwood, to be a composite of two distinct species. Therefore, Underwood had available to him at the time of his revision representatives of a maximum of seven taxa from five islands of the archipelago.

The salient features of Underwood's revision may be summarized as follows: he regarded assignment to species or subspecies level of isolated, allopatric forms to be largely a matter of taste; he believed color characters to be of primary importance in species recognition, and squamation characters to be "only indirectly significant by-products of species differentiation" (p. 193); he preferred to regard populations as subspecies when monophyletic relationship was "clear"; and finally, he believed that the general degree of morphological similarity and difference between two forms could be used as a reasonable indication of the clarity of their relationship.

Although I do not feel that there was consistent adherence to these principles in the annotated list of forms of the eastern

Caribbean presented by Underwood, the material he had available was extremely scant, to say the least, and it is therefore only to his last principle that I take exception at this point.

The validity of "degree of similarity" as an indication of relationship needs especial consideration before it can be used in the species group. In particular, it is demonstrably invalid with regard to sympatric species of *Anolis* in the West Indies. An example of this point can be found in Underwood and Williams (1959) with respect to the *grahami-opalinus* group in Jamaica: here Underwood (p. 47) himself acknowledges that the two intergrading subspecies of *Anolis grahami* are, in fact, considerably more morphologically divergent from each other than either is from the sympatric *Anolis opalinus*.

To me it seems that a principle such as "degree of similarity," so easily rejected for sympatric forms, should not be considered valid when applied to allopatric forms in the species group. "Degree of similarity" is in constant use with higher taxonomic categories, but one is reminded of Simpson's (1961) discussion of the fact that higher taxonomic categories are entirely man-made assemblages, and therefore of a wholly arbitrary nature. Morphological "degree of similarity" has, for these reasons, not been used in the following revision and description of Guadeloupéen *Anolis* as an indication of specific or subspecific rank. Acceptance of the "principle" would lead to the wrong conclusions in more than half the cases considered.

In revising the Guadeloupéen forms, and describing the previously unknown ones, I have used instead Simpson's definition of the "evolutionary species," in which the principal criterion is continuity of evolutionary role.

As Simpson carefully points out, geographic isolation tends to break the continuity of evolutionary role; thus isolated, allopatric forms may well be distinct species, even when derived from the same ancestor. In assigning populations to subspecific rank under the same species, in the Guadeloupéen archipelago, I admit the following as evidences of continuity of evolutionary role:

1. Actual intergradation: where there exists between two distinct populations occupying different geographic areas a zone in which "intergrade" individuals assure continuous gene flow between the two extremes.

2. The presence of a morphologically intermediate population,

when isolated by a topographical barrier, between the two extremes. This would include a series of geographically isolated, allopatric[1] populations which proceed in a stepwise sequence relative to the development or degeneration of characters in such a way that the second is intermediate between the first and third, the third is intermediate between the second and fourth, etc. — *even when the forms involved are 100 per cent distinct from each other.* A sequence of forms such as this will be referred to hereafter as a "stepped-cline" series, and in such cases I regard each member of the series as worthy of nomenclatural recognition providing it is diagnostically distinct from the others. In cases where it is not diagnostically distinct from the others I refer to it as though it were a population of actual intergrades.

3. Tenable evidence that the extant differences are the result of a trend in an isolated population of the species under which the different form is to be included. A case like this requires, to my way of thinking, the presence of some third population which, though demonstrably a member of the species involved on other bases, sets a precedent for evaluation of the sort of differences noted in the form presumed to have resulted from this trend. Examples of this are comparatively rare, and, I believe, constitute the only cases in which assignment to rank may degenerate to a matter merely of personal taste.

It is my belief, based on seven years of observing West Indian *Anolis,* both in the field and in the laboratory, that no two samples of specimens, no matter how different they appear, may be unfailingly allocated to correct rank relative to each other within the genus unless they are sympatric, or unless samples of geographically intermediate populations are available and considered. In the latter case, it must be remembered that, should the samples be found to represent members of the same evolutionary species, their status as distinct subspecies will depend entirely on whether or not they represent diagnostically homogeneous, clear-cut geographic segments of the same species. Two ends of a gradual cline, not broken into segments, or whose segments are not diagnostically distinct, are not herein regarded as nomenclaturally distinct, no matter how different from each other.

This is to say that *a great deal of geographic variation within species does not produce the sort of segmental units we can*

[1] The term "allopatric" is here used *sensu stricto,* and is not to be confused with "parapatric."

*usefully refer to as "subspecies."* The fact that a large number of geographic units which can be usefully regarded as subspecies are present in the Guadeloupéen archipelago is genuinely remarkable, and is considered under "Evolutionary Discussion."

## METHODS OF ANALYSIS

The primary materials for this study are 792 specimens of *Anolis* collected from 77 localities on 13 islands throughout the archipelago. During August and September of 1961, 755 specimens were collected from 73 localities, and the additional 37 specimens from four localities were collected in September of 1962 on two islands, to insure coverage of all distinctive populations. Specimens already in the Museum of Comparative Zoology (MCZ) were considered only after the living material had been examined.

Specimens were preserved, tagged, and catalogued only after careful color notes had been taken. Color sketches were made in the field of all the forms involved. All of the forms described herein were initially recognized on the basis of color characters. Scale characters, though often noticeable in the field, were not considered in detail until the specimens were studied in the laboratory. Fortunately, those characteristics of squamation which were noted in the field, as well as others discovered since, vary concordantly with the color characters, and are helpful in distinguishing the forms.

In attempting to render the females of the various forms more readily distinguishable, I have classified the middorsal patterns represented among female Guadeloupéen *Anolis* under five headings (see Figure 1):

1. *Broken:* A pale middorsal stripe set off from the dorsolateral coloration by a coalescing series of dark spots.
2. *Striped:* A pale middorsal stripe set off by a continuous dark border on each side.
3. *Ladder:* A middorsal pattern with dark transverse connections across the pale middorsal stripe from one border to the other.
4. *Mottled:* Light and dark middorsal markings not forming a special pattern.
5. *Obsolete:* A dark middorsal zone, without markings, contrasted to the dorsolateral coloration.

It was noted in the field that the females of the forms involved were not only distinctive relative to each other, but that the

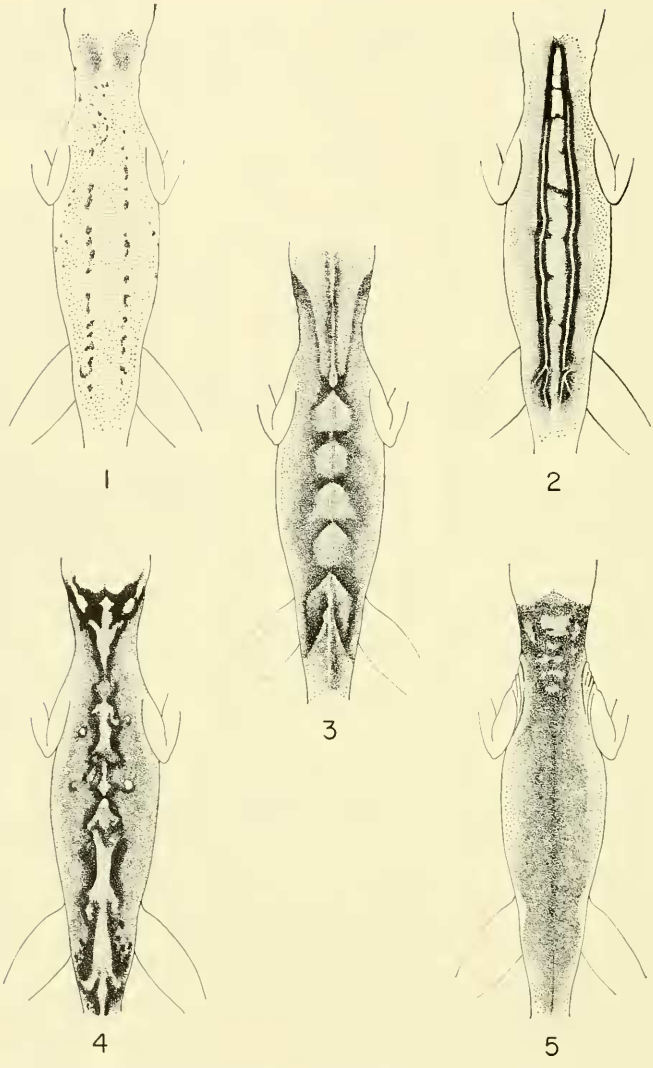


Figure 1. Middorsal patterns of female *Anolis marmoratus:* 1. broken (MCZ 71284); 2. striped (MCZ 70945); 3. ladder (MCZ 70676); 4. mottled (MCZ 71356); 5. obsolete (MCZ 71210). See text for explanation.

total coloration and pattern of the females was often more constant within any one taxon than these features in the males. Underwood did not deal with females simply because he regarded them as being only occasionally distinctive. I have not found this to be the case; on the contrary, the females in life are just as distinctive as the males. Also, males of some forms, from any one locality, are apt to show such a bewildering array of spots and marbles, varying from many and bold to very few and vague, that they can be genuinely confusing until one has come to recognize the constant, and often rather subtle, characters common to all specimens. Females were not found to differ from males with respect to squamation characters.

The following general characteristics of squamation were considered for all forms:

1. *Scale size.* That striking differences in scale size existed between several of the forms was noted in the field. In an attempt to render this character diagnostically useful, several methods of quantification were used. First, the number of dorsals in the standard distance (defined as the distance from the center of the eye to the tip of the snout) was counted and plotted against the number of ventrals in the standard distance in a two-variable linear graph. This method showed the differences anticipated, but was open to the criticism that head-body proportions might vary among the several forms. Consequently, the ratio of standard distance to snout-vent length was calculated for all specimens. The relationship proved quite constant: the standard distance is between 16 and 19 per cent of the snout-vent length in all Guadeloupéen anoles, except very old and very young specimens; in these exceptions the standard distance may be as little as 14.5 per cent of the snout-vent length. As a further check on the accuracy of the standard distance count method, the around-the-body count approach was utilized. Around-the-body counts, midway between axilla and groin, were made on all specimens from Ilet-à-Kahouanne, Ilet-à-Fajou, Les Iles de la Petite Terre, Marie Galante, and Les Iles des Saintes, as well as in scattered series from various localities on La Guadeloupe, Grande Terre, and Désirade: some 220 in all. This method showed the same differences between the same forms, and was sufficiently tedious to increase my appreciation of the practical value of the standard distance count.

In the following diagnoses of each form, the range of dorsal scales counted in the standard distance, based on all the specimens available from my collections, is given. The count is made between six and eight scales lateral to the middorsal line, and

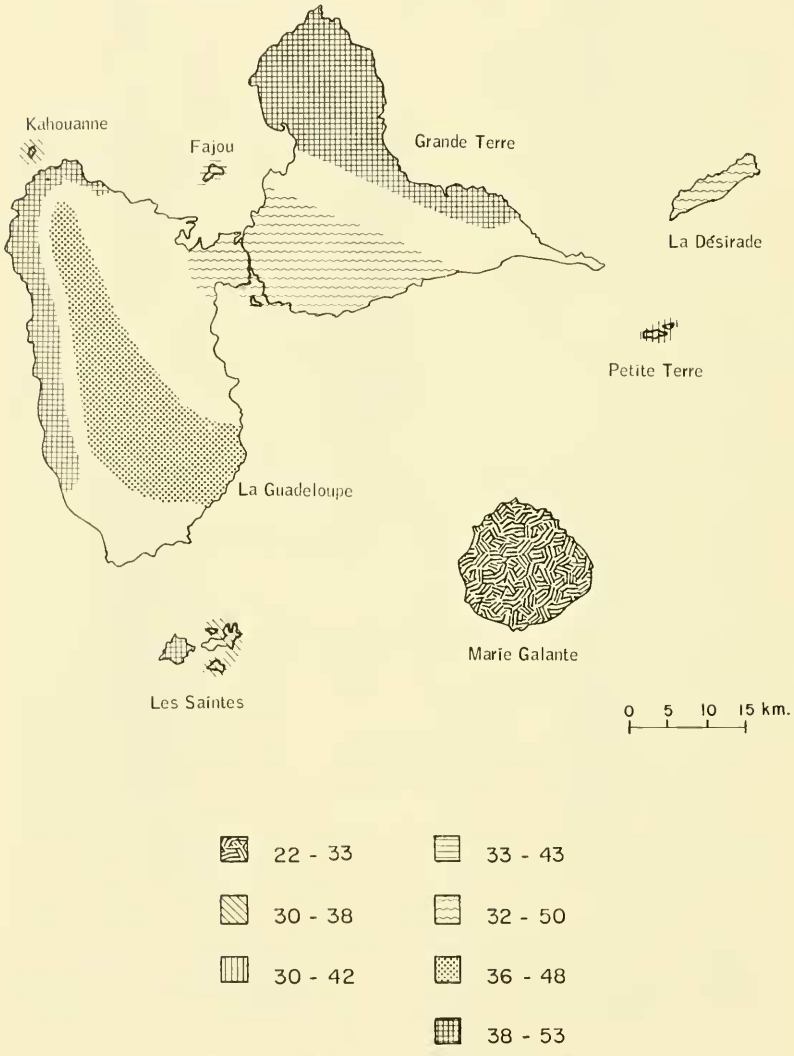


Figure 2. Geographic variation in number of dorsal scales contained in the standard distance at midbody. The major islands and island groups are here named for future reference.

parallel to that line. In each case the average for all the specimens counted was not more than ± 1 from the mean of the range given. Making the count in the manner outlined renders what might have been a most laborious sort of character as simple as possible, and yet shows quite well the differences noted between forms. (See Figure 2.)

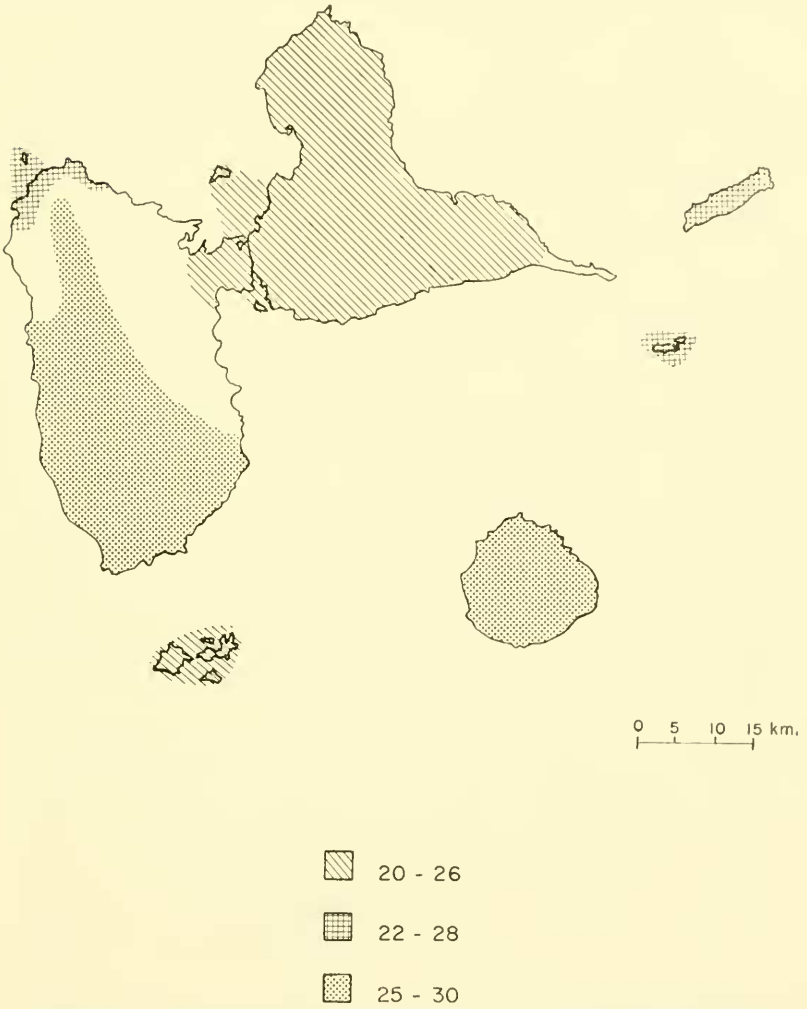


Figure 3. Geographic variation in number of subdigital lamellae under second and third phalanges of fourth toe. The major islands and island groups are named in Figure 2.

2. *Subdigital lamellae:* Lamellae were counted under the second and third phalanges of the fourth toe. The differences are averages, and not diagnostic, but the geographic variation with respect to this character has been mapped because the variation is real and concordant with the variation in other characters. (See Figure 3.)

## SYSTEMATIC DISCUSSION

Underwood recognized five named populations and one unnamed one as representatives of five distinct species, one with two subspecies; Williams would have added a sixth. In the present review all of those names regarded as valid by Underwood are retained, the Désirade anole he felt he could not properly name is described, and Williams' seventh form is accepted and described. I have, however, lowered all of them to subspecific rank under the same species. So that I may not immediately be scorned as a rabid lumper, let me point out that I have likewise described five more subspecies of the same species, making in all twelve subspecies.

*Anolis marmoratus* Duméril and Bibron, 1837, is the oldest available name for a Guadeloupéen anole. *A. marmoratus* may be distinguished from the adjacent forms by the following brief, species-level diagnoses:

*Anolis oculatus*, of Dominica, is an anole of the *bimaculatus* group, *sensu* Underwood, in which the prenasal scale borders on the rostral anteriorly and the anterior edge of a large nasal scale (entirely containing the naris) posteriorly; the prenasal is roughly quadrangular in shape. The ventrals are always at least faintly keeled, and the keels form lines that converge on the ventral midline posteriorly.

*Anolis marmoratus,* of the Guadeloupéen archipelago, is an anole of the *bimaculatus* group, *sensu* Underwood, in which the prenasal scale borders the rostral directly, extends posteriorly to or beyond the level of the anterior edge of the naris, and either borders the anterodorsal edge of the nasal, or itself forms the anterodorsal border of the naris. The ventrals may or may not be keeled, but if keeled at all the keels form lines converging towards (rarely ever reaching) the ventral midline, or parallel to it.

*Anolis lividus*, of Montserrat, is an anole of the *bimaculatus* group, *sensu* Underwood, in which the prenasal scale borders directly on the rostral, extends posteriorly to or beyond the level

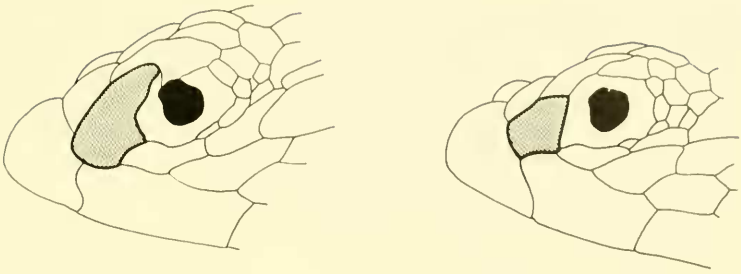

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Figure 4. Snout squamation in two species of *Anolis:* 1. *A. marmoratus* (MCZ 71202); 2. *A. oculatus* (MCZ 60364). The prenasal scale is shaded.

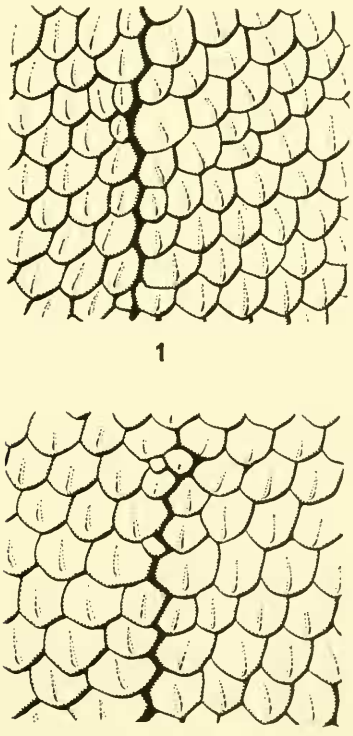

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Figure 5. Ventral keeling in two species of *Anolis:* 1. *A. lividus* (MCZ 6176); 2. *A. marmoratus* (MCZ 71202). In *A. marmoratus* the ventrals may be entirely smooth.

of the anterior edge of the naris, and either borders on the anterodorsal edge of the nasal, or forms the anterodorsal border of the naris itself — as in *A. marmoratus*. The ventrals are always at least faintly keeled, and while many lines of keels may converge on the ventral midline posteriorly, at least some, in the abdominal area, form lines which diverge.

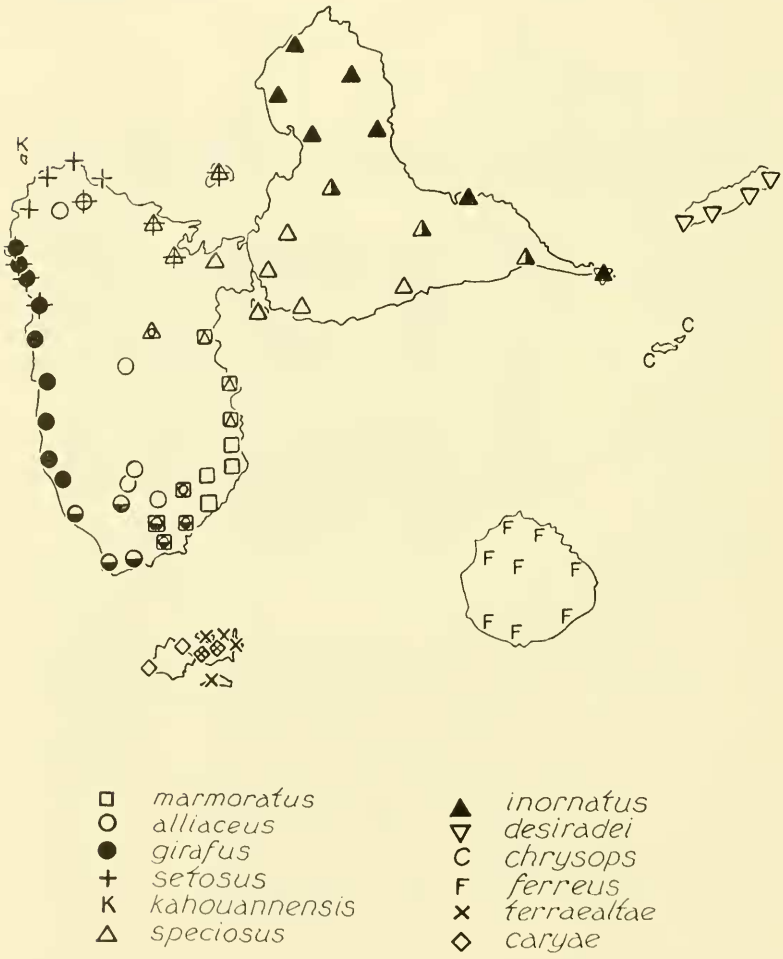


Figure 6. The ranges of the twelve forms of *Anolis marmoratus* in the Guadeloupéen archipelago. The major islands and island groups are named in Figure 2.

Figure 4 shows both conditions of the prenasal scales, and Figure 5 shows examples of the most confusing sorts of abdominal keeling. Using these characteristics, the three species may be separated without too much difficulty, regardless of age or sex. I have seen some specimens in which the prenasal was equivocal on one side, but it was always definitely one sort or the other on the other side, and provided the correct identification.

The ranges of the twelve forms recognized are mapped in Figure 6.

The nominate form of the Guadeloupéen species is:

ANOLIS MARMORATUS MARMORATUS Duméril and Bibron

*Anolis marmoratus* Duméril and Bibron, 1837, Érp. Gén. 4: 139.

*Holotype:* Muséum National d'Histoire Naturelle Ig. 43, no date, coll. Plée.

*Type locality:* "Martinique" (in error); herein revised to Capesterre, La Guadeloupe.

*Diagnosis:* Dorsal scales in the standard distance 36 to 48 (average 42); 25 to 30 (average 28) subdigital lamellae; adult male green, changing to brown; snout suffused with orange; head, neck, and orbital area boldly marbled with bright orange; throat fan light orange-yellow with yellow scales. Adult female green, with an obsolete middorsal pattern.

*Description:* MCZ 71202 is noted in my field catalogue as "the most beautiful anole I have ever seen." In life, this adult male was bright apple-green, shading to blue on the tail and yellow-green on the limbs. No flank stripe was present. On the neck and head the ground color shaded to blue-grey; the snout and head were broadly suffused with russet becoming in the temporal, orbital, and nape regions brilliant orange marbles, tending towards longitudinal stripes. The belly was lime-green. The throat fan was bright, pale orange-yellow with butter-yellow scales. In the dark phase the specimen assumed a deep chocolate-brown dorsally, became much darker ventrally — even to the extent of darkening the throat fan — but retained the orange marbling. Aside from the marbling on the head and neck, there were no markings. This specimen, the largest examined, was 77 mm in snout-vent length.

The adult female is grass-green, shading to grey or grey-brown on the head, middorsum, and tail, and with a lime-green belly. Aside from the contrast between the green of the sides

and the grey to grey-brown of the middorsum, producing the pattern I have termed "obsolete," there are no markings in life. Color change is merely from darker to lighter.

*Variation:* The extent of marbling varies in the adult male from all over the head and neck, to or beyond the level of the shoulder (as in the holotype), to restriction to the head region only. The suffusion of orange pigment anterior to the eyes, however, is constant in all, and the lack of it will serve to distinguish intergrades with other forms which may also show orange marbling. The ground color of the head varies from slatey blue-grey to powder blue-grey.

*Distribution:* This form is restricted to the plain of Capesterre, southwestern La Guadeloupe.

*Specimens examined:* MCZ 56043, "Guadeloupe" (Guesde coll.); MCZ 71179-93, Capesterre; MCZ 71194-201, Bananier; MCZ 71202-12, Routhiers; MCZ 71213-22, Carangaise.

*Discussion:* This spectacular anole has very narrow areas of intergradation to the west and south with the montane form and intermediates between the montane form and the southern leeward coast form. To the north, however, there is little barrier or ecological break, and a lengthy zone of intergradation with *speciosus* extends along the coast. MCZ 71140-43, from Grande Etang, *ca.* 400 meters elevation, are intergrades with *alliaceus,* the montane form. MCZ 71150-61 from Dolé, MCZ 71172-78 from Morne-à-Zailes, and MCZ 71162-71 from Trois-Rivières represent three-way intergrades between *marmoratus, alliaceus,* and the southern leeward coast form, *girafus.* MCZ 71136-39 from Ste. Marie, MCZ 71128-35 from Goyave, and MCZ 71113-27 from Petite Bourg represent intergrades with *speciosus,* which occupies the "waist" between La Guadeloupe and Grande Terre as well as southwestern Grande Terre.

### Anolis marmoratus alliaceus Cope

*Anolis alliaceus* Cope, 1864, Proc. Acad. Nat. Sci. Philadelphia, 175. Type: British Museum of Natural History (BMNH) 946. 8.28.96, no collector, no date.

*Anolis bimaculatus alliaceus,* Underwood, 1959, p. 199.

*Type locality:* None designated; here restricted to Maison Forestier du Matouba, elevation 700 meters, La Guadeloupe.

*Diagnosis:* Dorsals in the standard distance 36 to 48 (average 42); 25 to 30 (average 28) subdigital lamellae; adult male green with no blue or bluish pigment in this ground color;

palpebral area of orbit white in the light phase, changing to grey as the animal turns dark green; dark dots, tending to run together, scattered over the anterior and dorsal surfaces, and set off by pale cream borders; throat fan deep orange with green scales. Adult female green with mottled middorsal pattern and small light or dark dots anteriorly.

*Description:* An adult male, MCZ 71340, from the type locality, was pea-green and completely lacked the bluish tones apparent on the posterior body or tail in males of all other forms from La Guadeloupe. The orbital area was brown-green, but the edges of the lids (palpebral area) were white. Large blue-black dots, some running together to form short marbling, were present dorsally; these dots were set off by cream-yellow areas that blended abruptly into the pea-green ground color. A vague, cream-yellow flank stripe was indicated across the forelimb insertion. Dull yellowish green on the temporal region extended posteriorly to beyond the ear, and was set off by a dark brownish streak along the upper mandible and a similar streak through the eye. The throat fan was dark, dull orange with yellowish green scales. The belly was bright green. Color change involved a darkening of the ground color, obscuring the head streaking, but intensifying the contrast between the ground color and the cream-yellow borders of the dots. This specimen, the largest examined, measured 72 mm snout to vent. (See Figure 7.)

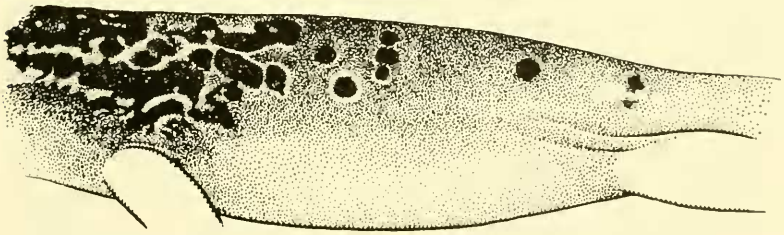

Figure 7. A representative pattern in adult male *Anolis marmoratus alliaceus* (MCZ 71340).

The adult female, in life, is duller green than the male, and shows a middorsal pattern of light and dark mottlings. Spots, small and sometimes indistinct, of dark or light pigment are present on the anterior trunk. The head streaking is usually present and notable.

*Variation:* The extent of dotting is extremely variable; some specimens are dotted and marbled extensively over the posterior nape, the shoulders and anterior middorsum; other specimens show only one indistinct dot in the region of the axilla. In some specimens the head streaking is indistinct. The complete lack of blue in the ground color, and the throat fan color combination, suffice to distinguish this form invariably from other green *marmoratus* even should a completely dotless specimen be encountered. The characters noted, as well as the bright green belly, serve to distinguish this form from the only other spotted anole on La Guadeloupe, the southern leeward coast form *girafus*. There is little variation in females.

*Distribution:* This form is restricted to rain forest in the central highlands of La Guadeloupe. It is strikingly arboreal and therefore difficult to collect, especially in climax forest, where the trees may reach 40 meters in height. None were seen at elevations higher than 900 meters.

*Specimens examined:* MCZ 61078-81, Matouba, 2000 ft. (= *ca.* 600m), nr. St. Claude (Proctor coll.); MCZ 71338-46, Maison Forestier du Matouba, 700 meters; MCZ 71347-55, Trace Victor Hughes, between Matouba and Grande Decouverte, *ca.* 850 meters; MCZ 71356, Etang-as-de-Pique; MCZ 71358-60, north ridge, Morne Moustique, *ca.* 650 meters. MCZ 71357, from Morne Goton, *ca.* 650 meters, has somewhat elongate dorsal scales, reminiscent of the north coast form, *setosus*. It is otherwise typical of *alliaceus;* Morne Goton is therefore taken to be the northern limit of the range of *alliaceus*.

*Discussion:* Intergradation with the nominate form has been discussed under that form. The montane anole, *alliaceus*, intergrades with *speciosus* between the "waist" and the central highlands at Vernou (MCZ 71144-49). Intergrades with *setosus* of the north coast are represented by MCZ 70883-4. from Sofaia, *ca.* 400 meters. Intergradation with the southern leeward coast form, *girafus*, is extensive and has caused the greatest confusion possible. This has been true because both are spotted forms, and the zone of intergradation includes both the towns of Basse-Terre (MCZ 71231-44) and Ste. Claude (MCZ 71287-303) — the two largest settlements on the island of La Guadeloupe. Evidence of *alliaceus* influence is present at sea level east of Basse Terre: MCZ 71223-48, from Delgres, and MCZ 71245-58, from Vieux Fort are intermediate series. This interesting region, where montane influence extends right to the coast, will

be considered under "Evolutionary Discussion." Typically, the intermediates show a pattern closely approaching *alliaceus* and coloration similar to *girafus*. Underwood's description of BMNH 1946.8.28.96, the holotype, does not rule out the possibility that this specimen may have come from this intermediate, southern tip population. Assignment of the name *alliaceus* to the montane form is, therefore, arbitrary, but supported by the described resemblance of the holotype's pattern to that of the montane form (the holotype's coloration in life is, of course, not available for discussion). In reality, these two forms are not confusingly similar, even in preservative, but very careful attention must be paid to their diagnostic characteristics if confusion, due to the spotted pattern generally present in both, is to be avoided. This is an example of a case where obvious, bold markings can be more confusing than useful simply because they are variably present in both forms, whereas more subtle characters can always be relied upon to be consistent and definitive.

### Anolis marmoratus girafus[1] subsp. nov.

*Holotype:* MCZ 71259, collected 14 August 1961 by J. D. Lazell, Jr.

*Type locality:* Vieux Habitants, La Guadeloupe.

*Diagnosis:* Dorsals in the standard distance 38 to 53 (average 47); 25 to 30 (average 28) subdigital lamellae; adult male blue-green to brown, always browner on the head and neck and always at least bluish on the posterior body and tail base; pale streaks and stipples, usually running together to form stripes that produce a reticulate pattern isolating dark spots, on the lateral trunk; throat fan pumpkin yellow with cream-colored to white scales. Adult female pale grey-brown with broken middorsal pattern.

*Description of holotype:* This adult male was warm brown on the head and neck, somewhat mottled with darker grey-brown. Posteriorly the ground color was pale blue-green, becoming bluer on the base of the tail. On the sides of the neck, in the axillary region, and along the lower costal region were dark grey-brown, polygonal spots separated by a pattern of broad, pale, cream to bluish reticulations which blended with the posterior ground

[1] The name *girafus* has been invented to indicate the reticulate pattern.

color. The belly was dirty white. The throat fan was bright pumpkin yellow with white scales. (See Figure 8.)

*Variation:* This is the most variable form on La Guadeloupe. As with *A. o. cabritensis* on Dominica (see Lazell, 1962, p. 470), there is some correlation of variation and geography. In the southern part of the range specimens are often quite bright blue-green and have a well developed pattern of reticulations that sometimes leave only a few, well-isolated dark dots in the axillary region. In the northern part of the range many specimens have merely several series of light spots along the sides which, though they coalesce, fail to produce a very reticulated pattern; northern specimens are also rather bright greenish. In the central portion of the range there is a dilution of green to the point where often only a faint blue tinge remains on the posterior body and tail base of an otherwise dingy grey-brown anole; too, in the central part of the range, the entire animal may be so dingy that the light spots and reticulations only show up in strong contrast when the animal is in the dark phase. There are no sharp breaks in this variation, and, in fact, specimens that approach all of the described variations can be collected in any part of the range. Therefore, though there are average differences in color pattern, the clinality and inconsistency of this variation precludes dividing this form up into a number of races with smaller ranges. All specimens from all parts of the range fit the diagnosis given for the subspecies. Some pattern variants are shown in Figure 8.

The adult females vary from fawn-brown to ash-grey, and have a paler middorsal stripe set off by coalescing dark spots. This produces what I have called the "broken" middorsal pattern.

*Distribution: A. m. girafus* occurs along the leeward coast of La Guadeloupe from just northwest of Basse-Terre to Malendure. This is the driest region on La Guadeloupe, and perhaps in the entire archipelago. It corresponds, as has been pointed out, with the northern leeward coast of Dominica. Convergence between the anoles occupying these two areas will be considered under "Evolutionary Discussion."

*Paratypes:* MCZ 71260-77, same data as the type; MCZ 71278-86, Baillif; MCZ 71304-18, Marigot; MCZ 71319-28, Boulliante; MCZ 71329-37, Malendure.

*Discussion:* Intergradation with *alliaceus* has been discussed under that form. *A. m. girafus* also intergrades with the north

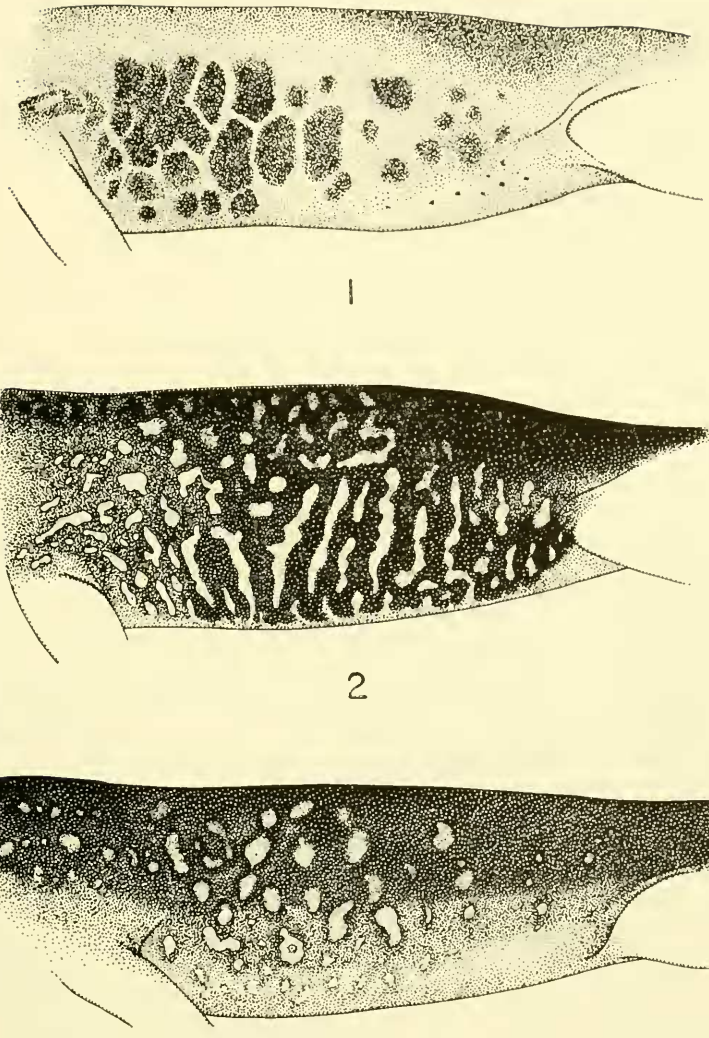


Figure 8. Pattern variation in adult male *Anolis marmoratus girafus*: 1. MCZ 71529, the type; 2. MCZ 71331; 3. MCZ 71304.

coast form, *setosus*, at the following localities: Anse Caraibe: MCZ 70850-58; Pointe Noire: MCZ 70841-49; Trou-Caverne: MCZ 70859-68; Ferry: MCZ 70869-82. These intergrades tend to extremes: from any one locality within the zone of intergradation one may collect specimens that closely resemble either *girafus* or *setosus*, though the majority show a variable combination of characteristics.

### Anolis marmoratus setosus[1] subsp. nov.

*Holotype:* MCZ 70813, collected 11 August 1961 by J. D. Lazell, Jr.

*Type locality:* Pointe Allègre, La Guadeloupe.

*Diagnosis:* Dorsals in the standard distance 38 to 53 (average 47); 22 to 28 (average 25) subdigital lamellae; dorsal scales spinose, those of the nape region so much taller than broad that a distinctly furred effect is produced; adult male blue-green with sooty transverse markings and a dark stripe through eye indicated when changing to the dark phase; throat fan yellow with greenish scales; belly pale, but without yellow tint. Adult female without a middorsal pattern as such, but with a variegation of green, brown, slate, and white speckles and blotches on dorsum, and bold, dark streaks on the lateral venter.

*Description of holotype:* This adult male was a nondescript green lizard immediately distinctive only because of the most peculiar character of the squamation. The dorsal ground color was green, shading to blue-green posteriorly and with some bluish wash on the head. The sooty transverse markings were not apparent except when changing from the light to the dark phase, or *vice versa*. The stripe through the eye was, however, noticeable in any phase. The belly was pale green; the throat fan was bright yellow with greenish or grey-green scales. Color change was to much darker, rendering the specimen almost black dorsally, and obliterating the dorsal markings — which, though diagnostic, seem to be never more than temporary. The type had several clusters of one to six bright yellow scales on the neck in no particular arrangement. The squamation is the most distinctive feature. It is, nevertheless, difficult to describe. The dorsals are conical to the point of being spines; this condition is accentuated in the nape region, and quite literally gives the

[1] *Setosus*, Latin, for "bristly."

most furred effect imaginable on an anole (see Figure 9). The holotype, the largest specimen examined, measured 66 mm snout to vent.

*Variation:* The diagnostic color pattern and squamation are quite consistent, but the amount of blue varies from the condition described for the holotype to a general blue wash. The peculiar clusters of yellow "spines" (scales) on the neck appear only in occasional adult males and are not relevant to the taxon.

The adult female is variable but always variegated and lacks a genuine middorsal pattern. The ground color is blotchy green, and brown, slate-grey, and pale grey or white mottles and blotches are present. There are bold, dark series of stipples forming streaks along the sides of the otherwise dirty white venter.

*Distribution:* This form is confined to the northern coast of La Guadeloupe.

*Paratypes:* MCZ 70814-19, same data as the type; MCZ 10403-27, Ste. Rose (Noble coll.); MCZ 70804-12, Ste. Rose; MCZ 70820-32, Deshaies; MCZ 70833-40, Rifflet.

*Discussion:* It was specimens of this form, plus intergrades between *alliaceus* (*sensu* Lazell) and *girafus,* that constituted Underwood's concept of *alliaceus.* As Underwood noted, Williams regarded the Ste. Rose series as distinct. Williams (pers. comm.) was on the verge of describing the Ste. Rose series as a distinct species because of the remarkable squamation when the first shipment of my anoles from the Guadeloupe region arrived; this shipment contained intergrades between *setosus* and *speciosus,* as well as the other two forms *setosus* touches on. Credit for its most apt and descriptive name, however, remains with Ernest E. Williams.

Intergradation with *alliaceus* and *girafus* has been discussed under those forms, respectively. Intergrades between *setosus* and *speciosus* occur along the extreme northeast coast of La Guadeloupe between Lamentin (MCZ 70988-96) and Morne Rouge (du Nord) (MCZ 70997-1003).

The population on Ilet-à-Fajou, intermediate generally between *setosus* and *speciosus,* requires discussion separately. MCZ 71004-13 from Ilet-à-Fajou fit the diagnostic color characters of *speciosus* (see diagnosis of that form) quite closely. I would have included them, therefore, under this form except that E. E. Williams pointed out the rather spinose character of their squamation. The combination of *setosus*-type squamation and *speciosus*-type coloration and pattern is common in

mainland intergrades between these two forms, and it is quite plausible to speculate that the Ilet-à-Fajou population was derived from a few specimens, from the adjacent coast, which had this combination; this might explain its consistency in Ilet-à-Fajou anoles. A careful examination of these anoles, however, revealed another interesting fact: they possess rather large scales — there being only 33 to 43 (average 37) contained in the standard distance. Since the character is not diagnostic, it fails to differentiate this population as a taxon, but indicates that a trend towards abnormally large scales may be expected in *Anolis marmoratus* populations confined to very small islands. I have tentatively assumed that this characteristic can, in fact, be expected, and on that entirely shaky foundation classify the following form as:

ANOLIS MARMORATUS KAHOUANNENSIS subsp. nov.

*Holotype:* MCZ 70791, collected 28 August 1961 by J. D. Lazell, Jr.

*Type locality:* Ilet-à-Kahouanne, Guadeloupe Passage, NW of La Guadeloupe.

*Diagnosis:* Dorsals in the standard distance 30 to 38 (average 33); 22 to 28 (average 25) subdigital lamellae; dorsal scales conical, producing a bulldog-collar-spike effect on the nape; adult male chartreuse (= bright yellow-green) with no markings except bluish washes on the head and chin; belly bright yellow; throat fan bright yellow with yellow scales. Adult female chartreuse with a bright yellow belly and no markings except occasional traces of a ladder middorsal pattern.

*Description of holotype:* In my field catalogue I have described this adult male as "a solid, brilliant chartreuse anole. Changes to dark green but never has any markings." There was a bluish wash on the snout and temporal region which continued onto the chin and anterior edge of the throat fan. The throat fan was pumpkin-yellow with bright yellow scales. The belly was butter-yellow. The orbital region was pale. Color change, as noted, was merely to darker. The scales are extremely large, and the difference between them and the scales of mainland anoles may be readily noticed in the field. Combined with their large size is the *setosus*-like characteristic of spinosity (though not to nearly so great an extent); the effect of conical, spike-like dorsal scales, especially on the nape, is striking (see Figure 9). The holotype, the largest specimen examined, measured 76 mm snout to vent.

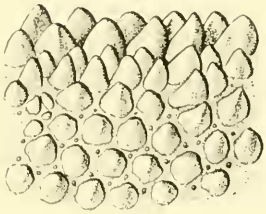

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Figure 9. Nape scales just lateral to the dorsal midline in two forms of *Anolis marmoratus:* 1. *kahouannensis,* type (MCZ 70791); 2. *setosus,* type (MCZ 70813).

*Variation:* The extent of blue wash on the heads of males varies from the condition described for the holotype to virtually absent. One specimen (MCZ 70792) darkened in blotches when changing to the dark phase; this was only vaguely reminiscent of the condition visible in *setosus.*

The adult female is almost completely without markings. There is no mottling, stippling, or streaking, though occasional segments of the ladder middorsal pattern characteristic of the young female may be retained in sexually mature individuals. The basic color is pea-green, and the belly is bright yellow.

*Distribution:* This anole is confined to Ilet-à-Kahouanne.

*Paratypes:* MCZ 70792-803, same data as the type.

*Discussion:* Assignment to subspecific rank under *marmoratus* is, in this case, an arbitrary action supported only by direct evidence, in the Ilet-à-Fajou population, that a tendency towards large scale size *can* occur in small, isolated *marmoratus* populations. Because the Ilet-à-Fajou population does demonstrate that enlarged scale size is within the potential evolutionary role of

*marmoratus*, it is at least possible to regard *kahouannensis* as a subspecies of *marmoratus* with respect to this character.

It is, however, disquieting to note that *kahouannensis* is 100 per cent distinct on the basis of coloration in life, quite apart from the scale size discrepancy. In the final analysis, there is no conclusive argument for the inclusion of this form within the *marmoratus* species; there is, nevertheless, a tenable argument that it should be included, since all of the mainland Guadeloupéen forms are 100 per cent distinct on the basis of coloration in life if intergrades are not considered. *A. m. kahouannensis* has no possibility of producing an intermediate population with the mainland forms, but I have, nevertheless, accepted it as a subspecies of *marmoratus* because such a judgment is tenable and because in my own opinion *kahouannensis* is not more distantly related to *setosus* than *setosus* is to those mainland forms with which it intergrades directly. My opinion is based on a general impression of these taxa both in life and after preservation; it is thus the sort of opinion that can neither be proven nor disproven on the basis of present information. Authors who wish to regard this form as a species distinct from *marmoratus* can find ample justification for doing so. However, the Kahouanne Island anole resembles *setosus* with regard to the convexity and spinosity of the dorsal scales, and fits *A. marmoratus* generally with regard to the prenasal and the ventral keeling.

### Anolis marmoratus speciosus Garman

*Anolis speciosus* Garman, 1887, Bull. Essex Inst., 19:45. Cotypes: MCZ 6172, 70947-50.

*Lectotype:* Here designated as MCZ 6172, collected by Richardson, March, 1886.

*Type locality:* "Marie Galante" (in error); here revised to Pointe-à-Pitre, Grande Terre.

*Diagnosis:* Dorsals in the standard distance 32 to 50 (average 40); 20 to 26 (average 23) subdigital lamellae; adult male green, without dorsal markings; venter brightly washed with yellow; orbital area sky-blue; throat fan sulfur-yellow with greenish scales. Adult female olive with ladder or striped middorsal pattern.

*Description:* MCZ 70961, an adult male from Pointe-à-Pitre, in life was bright green over the entirely unmarked dorsum.

The venter was entirely washed with bright yellow, producing a deep yellow-green zone along the sides. The orbital skin was sky-blue, and sharply set off from the green color of the rest of the head. The throat fan was sulfur-yellow with green-grey scales. This male had several clusters of yellow scales scattered on the sides of the neck, reminiscent of some *setosus* males. The scales of the dorsum are not spinose (i.e. never taller than broad), and closely resemble the dorsal scales of anoles (excluding *setosus*) from La Guadeloupe. Color change involved merely a darkening of the ground color to slatey-green, accompanied by greying of the orbital skin. This specimen, the largest examined, measured 71 mm in snout-vent length.

The adult female is olive-green, has a striped or ladder mid-dorsal pattern, and lacks other distinctive markings including a flank stripe.

*Variation:* This form is remarkably constant in color characters. As with *setosus,* the presence of yellow scale clusters on the neck is occasional in old adult males and not relevant to the taxon. Specimens from Ilet-à-Cochons and the south coast of Grande Terre sometimes show a more gradual blending of the blue coloration of the orbital region with the green of the head than do specimens from the more northern portions of the range. There is, however, never a dark stripe through the eye, as in *setosus.*

*Distribution:* This form occurs throughout SW Grande Terre (i.e., the wetter area of this island), on the "waist" between Grande Terre and La Guadeloupe, and on Ilet-à-Cochons (sometimes called, uncomplimentarily enough, Ilet-à-Gouvernement).

*Specimens examined:* MCZ 6172, "Marie Galante," Lectotype (Richardson coll.); MCZ 70947-50, "Marie Galante," Paralectotypes (Richardson coll.); MCZ 70913-24, Abymes; MCZ 70925-34, Gosier; MCZ 70935-46, Ste. Anne; MCZ 70951-60, Baie Mahault; MCZ 70961-77, Pointe-à-Pitre; MCZ 70978-87, Ilet-à-Cochons, ou Gouvernement.

*Discussion:* The locality of this form given by Garman (presumably *fide* Richardson) in the original description is incorrect. The five males in the type series (MCZ 6172, 70947-50) fit quite precisely with the form from SW Grande Terre on squamation characters and are powder-blue from long preservation. They completely lack markings such as the faint flank stripe and brown head (which does not turn blue in preservative) that characterize the NE Grande Terre population, the only other form that these long-preserved specimens might conceivably be

confused with. Richardson demonstrably collected in both Désirade and Marie Galante. It would have been remarkable indeed if he had failed to stop at the large and busy port of Pointe-à-Pitre while in this area. To add to the evidence against the "Marie Galante" locality is the fact that no specimen resembling *speciosus* has ever been collected there since, whereas the Marie Galante anole, *ferreus*, is common indeed — though its original type locality was cited as "Guadeloupe."

Intergradation with nominate *marmoratus*, *alliaceus*, and *setosus* has been discussed under those forms, respectively. Intergradation with the dry country form of NE Grande Terre, *inornatus*, occurs along a line through Morne-a-L'Eau (MCZ 70885-94), Chateau Gaillard (MCZ 70895-902), and St. François (MCZ 70903-12).

### Anolis marmoratus inornatus[1] subsp. nov.

*Holotype:* MCZ 71036, collected 13 August 1961, by J. D. Lazell, Jr.

*Type locality:* Anse Bertrand, Grande Terre.

*Diagnosis:* Dorsals in the standard distance 38 to 53 (average 47); 20 to 26 (average 25) subdigital lamellae; adult male pale grey-green on trunk, rich brown on head; orbital area brown; belly pale lime-green; throat fan yellow with white to cream-colored scales; flank stripe indicated. Adult female pale grey-brown with striped middorsal pattern and flank stripe.

*Description of holotype:* This adult male was pale green with a bluish tinge on the posterior body and tail base. The head was warm brown; the orbital skin golden brown. The brown of the head graded gradually into the green of the dorsum. There were faint, grey-brown vermiculations on the nape. The belly was pale, dirty green posteriorly, becoming lime-green in the chest region. The throat fan was dull yellow with white scales. A flank stripe, paler grey-green than the dorsal ground color, extended from the shoulder to the hind limb insertion. There were faint indications of darker grey-brown transverse markings across the dorsum. The slight color change involved a general trend towards becoming darker and browner. This specimen, the largest examined, measured 75 mm snout to vent.

*Variation:* This form is rather variable. Some specimens lack all signs of neck vermiculations or transverse markings. The

[1] *Inornatus*, Latin, for "unadorned."

amount of green varies from the condition described for the holotype to one in which it is virtually restricted to the posterior belly and rump regions. In most specimens the throat fan appears to have a paler yellow border and a brighter yellow center, and the scales of the fan are often closer to cream-color than white. The variation is individual and does not correspond to different localities within the range of the form.

The adult female is pale tan to ash-grey on the dorsum, and always brownish on the head. The striped middorsal pattern is not bold but is always noticeable. A definite flank stripe is indicated in the thoracic region.

*Distribution:* This form occurs throughout northern Grande Terre and extends southeastward along the northeast coast of that island towards, but not to, Pointe-des-Chateaux.

*Paratypes:* MCZ 71037-42, same data as the type; MCZ 61082-92, Moule (Proctor coll.); MCZ 71014-19, Moule; MCZ 71020-25, Petite Canal; MCZ 71026-35, Port Louis; MCZ 71043-48, Campeche; MCZ 71049-57, town of Ste. Marguerite.

*Discussion:* Intergradation with *speciosus* has been discussed under that form. The population on the Pointe-des-Chateaux peninsula requires especial consideration. The males from this area show definite vermiculation on the nape, and usually a few bold, dark spots at least in the dark phase. There is a noticeable yellow wash along the sides and the orbital skin has a distinctly orangish tone in some specimens. In keeping with the norm of intergrade populations in the archipelago, these anoles are very variable: some closely resemble *inornatus* in important respects, others closely approach the anole found on the adjacent island of La Désirade. Therefore, MCZ 71058-67, from Pointe-des-Chateaux, are regarded as a sample of an intermediate population between *inornatus* and the following form:

### Anolis marmoratus desiradei subsp. nov.

*Holotype:* MCZ 71068, collected 14 September 1961, by J. D. Lazell, Jr.

*Type locality:* Grande Anse, La Désirade.

*Diagnosis:* Dorsals in the standard distance 32 to 50 (average 40); 22 to 28 (average 25) subdigital lamellae; adult male pale greenish with yellow wash on sides and yellow belly; dorsal surfaces extensively vermiculated with darker grey-brown; throat fan yellow with white to cream-colored scales; orbital area bright

rust-red; chin yellow with bold blue-grey streaking. Adult female grey-greenish with grey head and yellow belly; middorsal pattern obsolete.

*Description of holotype:* This adult male was pale grey-green boldly vermiculated with dark grey-brown all over the dorsal surfaces of the trunk and legs. The lateral surfaces were washed with yellow, and the belly was bright yellow. A lack of vermiculation along the side indicated a vague flank stripe. The chin was yellow and blue-grey bars ran from the anterior base of the throat fan to the infralabials. The head was dull brown to grey-brown, and the bright rust-red of the orbital skin stood out in bold contrast. The throat fan was yellow with cream-colored scales. Color change involved general darkening and increased brownness; the vermiculations became especially bold in the dark phase. The holotype, the largest specimen examined, measured 80 mm snout to vent.

*Variation:* There is a definite cline in extent of yellow on the sides and in the ground color, increasing as one proceeds eastward along La Désirade. Some specimens from all over the island show small orangish patches on the nape and anterior body; this is by no means constant and not characteristic of the taxon.

The adult female is distinctly grey on the head and becomes greener posteriorly. There is no indication of vermiculation. The belly is distinctly yellow. Young specimens show a vague striped middorsal pattern, but those apparently mature females were somber grey middorsally, producing the pattern I have called obsolete.

*Distribution:* This form is confined to the island of La Désirade.

*Paratypes:* MCZ 57285-96, "Desirade Id." (Richardson coll.); MCZ 62210-1, Ravine la Rivière (Proctor coll.); MCZ 62212, Le Calvaire (Proctor coll.); MCZ 62213-17, Grande Anse (Proctor coll.); MCZ 71069-77, Grande Anse; MCZ 71078-87, Pointe-des-Colibris; MCZ 71088-100, Le Souffleur; MCZ 71101-12, Pointe Double.

*Discussion:* The intermediate population between *inornatus* and *desiradei* has been discussed under that form. It need only be pointed out here that this population, while not one of "intergrades" as such, precludes the possibility of recognizing *desiradei* as a species distinct from *marmoratus:* on Pointe-des-Chateaux, Grande Terre, some anoles that are unequivocally *marmoratus* show *desiradei* characteristics.

Beginning with *desiradei* there is a stepped-cline series through the "satellite" islands of the archipelago. The first population of this series is:

ANOLIS MARMORATUS CHRYSOPS[1] subsp. nov.

*Holotype:* MCZ 70649, collected 4 September 1961, by J. D. Lazell, Jr.

*Type locality:* Terre de Haut, Les Iles de la Petite Terre.

*Diagnosis:* Dorsals in the standard distance 30 to 42 (average 36); 22 to 28 (average 25) subdigital lamellae; adult male somber green-grey with bright yellow suffusion on the sides and bright yellow belly; vermiculations present on the anterior trunk and nape, at least, and dark dotting usually present on remaining dorsal surfaces; orbital area red-gold; chin entirely blue-grey; throat fan yellow with pale yellow scales. Adult female grey with yellow belly, an obscure striped middorsal pattern, and a brief flank stripe.

*Description of holotype:* This adult male was grey-green, becoming greener posteriorly and virtually grey (or grey-brown) on the head. The yellow of the venter extended as a bright suffusion over the lateral trunk. The vermiculations tended to break up into small speckles on the posterior body and hind limbs; no notable lack of vermiculation distinguished a flank stripe region. The chin was entirely blue-grey, and the skin of the orbital area was red-gold. Color change was merely to slightly darker and browner. The holotype, the largest specimen examined, measured 73 mm snout to vent.

*Variation:* The extent of vermiculation and its break-up into speckling is rather variable, but specimens always show vermiculation as such at least on the nape and anterior trunk. Some specimens showed a vague indication of the vermiculation-free flank stripe area, though this region is usually heavily invaded with yellow. The color of the orbital skin and the uniformity of the blue-grey chin are constant features.

The adult female is distinctly duller and greyer than the average *desiradei* female and retains the striped middorsal pattern. The contrast between the grey of the head and the green-grey of the dorsum is not marked, though the belly is bright yellow. A short flank stripe is present.

*Distribution:* Terre de Haut and Terre de Bas, Les Iles de la Petite Terre.

[1] *Chrysos*, Latin, for "gold," plus *ops*, Greek, for "appearance."

*Paratypes:* MCZ 70656-65, same data as the type; MCZ 70650-5, Trou Canard, Terre de Bas, Les Iles de la Petite Terre.

*Discussion:* The Petite Terre anole agrees with *desiradei* in possessing vermiculations, though they are reduced from the condition in that form; it agrees, on the other hand, with *ferreus* in having a uniform blue-grey chin, though the blue-grey does not extend onto the throat fan, as it usually does in *ferreus*. The orbital skin color, though entirely distinctive, is what one would expect of a mixture between the rust-red of *desiradei* and the dull yellow of *ferreus*. The extent of yellow on the lateral surfaces is likewise intermediate between these two forms. Dorsal scale size shows a marked overlap with *desiradei*, on the one hand, and *ferreus*, on the other. Some adult males have the neural spines of the caudal vertebrae distinctly more elongate than in any *desiradei* and as elongate as in some *ferreus*. Therefore, in every respect except maximum snout-vent length (in the sample available), *chrysops* is morphologically intermediate between two extremes: *desiradei* and *ferreus*.

In contrast with the Ilet-à-Fajou population, which is also an isolated morphological intermediate, *chrysops* is entirely distinctive in its own right; there is no intergrade population with which *chrysops* individuals could be confused, and there are diagnostic characteristics by which *chrysops* may be unequivocally distinguished. For these reasons *A. m. chrysops* is granted nomenclatural rank. Because it is an intermediate population between *A. m. desiradei* and *ferreus* of Marie Galante and because it is geographically intermediate as well, it connects the Marie Galante anole with the remainder of the *marmoratus* series, and *ferreus* must therefore be regarded not as a distinct species but as:

### Anolis marmoratus ferreus (Cope)

*Xiphosurus ferreus* Cope, 1864, Proc. Acad. Nat. Sci. Philadelphia, 168. Type: BMNH 1946. 8.5.59., no collector, no date.

*Anolis asper* Garman, 1887, Proc. Essex Inst., 19: 31. Syntypes: MCZ 6162. (Type locality Marie Galante.)

*Type locality:* "Guadeloupe" (in error); here revised to Morne Constant, Marie Galante.

*Diagnosis:* Dorsals in the standard distance 22 to 33 (average 28); 25 to 30 (average 28) subdigital lamellae; adult male somber grey-brown becoming greener posteriorly; dorsum sprinkled with dark dots seldom coalescing to form short vermiculations; suffusions, often forming blotches, of yellow laterally;

orbital area dull yellow; uniform blue-grey of chin often invading otherwise yellow throat fan with yellow scales. Adult female grey-brown to greenish with brief flank stripe, obsolete middorsal pattern, and a very pale yellowish belly.

*Description:* An adult male from Morne Constant was dingy grey-brown shading to brownish blue-green on the tail and dull blue-grey on the head. The sides were suffused with rich yellow, forming large blotches anteriorly. The venter was duller, paler yellow. The chin was entirely blue-grey, and this color invaded the anterior quarter of the throat fan; the remainder of the throat fan was bright yellow with yellow scales. The orbital region was dull yellow, strikingly distinct from the blue-grey of the snout, though less abruptly blending into the browner grey of the temporal region. The nape and dorsum were liberally speckled with dark grey-brown. This specimen, MCZ 70748, shows a remarkably high tail crest, and, in life, had three to five longitudinal chestnut-brown stripes along that crest. This specimen measured 99 mm snout to vent, though a specimen from Vieux Fort (the largest examined), MCZ 70767, measured 119 mm snout to vent, thus 21 mm larger than the largest *ferreus* previously recorded (Underwood, 1959, p. 203).

The adult female is usually much greener than *chrysops* and always lacks the brightness of the yellow belly. Large specimens have the striped middorsal pattern reduced to obsolescence: a short flank stripe, in the shoulder region, is noticeable.

*Variation:* The speckling ranges from the condition described above to but a few scattered stipples, covering one to four scales, in the nape region: thus, from nearly the condition of *chrysops* to nearly the condition of *terracaltae* (which completely lacks speckling or stipples). The extent of yellow suffusion and the presence of yellow blotches on the anterior trunk actually varies from the condition of *chrysops* to that of *terracaltae*, and is less distinctive. The height of the caudal crest, even in old males, is extremely variable and cannot be used to delimit the taxon; likewise, the presence of longitudinal streaking along the tail crest is merely an occasional character and not relevant to the taxon. Throat fan coloration varies tremendously; the condition described for MCZ 70748 is very common, but the fan may be entirely yellow without blue-grey invasion, sharply divided in half between the two colors, or largely grey with yellow reduced to the posterior portion. One specimen, MCZ 70769, had an entirely blue-grey throat fan. In view of my experience with *ferreus* in the field, Barbour's description of

the throat fan as grey with a wide lemon yellow margin (Underwood, 1959, p. 203) is puzzling. It is suggested that Barbour added this note as an afterthought, based on a combined recollection of some *ferreus* with bicolored fans and the fact that other anoles with bicolored fans often have an arrangement of center-color contrasted to margin-color.

Females are likewise variable; young specimens look very much like the female anole from Terre de Bas, Les Iles des Saintes, though they would show an absolute scale size discrepancy with that form. Older specimens are notably darker and often greener than females of adjacent populations and often show a definite bluish tinge.

*Distribution:* This form is confined to the island of Marie Galante.

*Specimens examined:* MCZ 6162 (17), "Marie Galante" (Richardson coll.); MCZ 28526-50, "Marie Galante" (Barbour coll.); MCZ 61093-95, 62218-27, St. Louis (Proctor coll.); MCZ 62228, Les Sources (Proctor coll.); MCZ 70748-58, Morne Constant; MCZ 70759-61, Capesterre; MCZ 70762-66, Grand Bourg; MCZ 70767-71, Vieux Fort; MCZ 70772-78, Ste. Germaine; MCZ 70779-84, Grelin; MCZ 70785-90, Pointe-des-Basses.

*Discussion: Anolis marmoratus ferreus* is the end of a cline in scale size and extent of blue-grey chin pigment that begins on Désirade; with respect to the extent of yellow on the lateral surfaces and dorsal marking it is intermediate between *chrysops* and the form next to be discussed, *terracaltae*. As with *chrysops*, *terracaltae* overlaps *ferreus* broadly in scale size, and even somewhat in the height of the neural spines on the caudal vertebrae. With respect to some characters, then, *terracaltae* is the continuation of the cline southwestward from Désirade; with respect to most of its other characters it is intermediate between *ferreus* and the final population of *marmoratus: caryae* of Terre de Bas, Les Iles des Saintes.

### Anolis marmoratus terraealtae Barbour

*Anolis terraealtae* Barbour, 1915, Proc. Biol. Soc. Washington, 28: 76. Type: MCZ 10627, collected by Noble, no date.

*Type locality:* "Terre d'en Haut, Iles des Saintes"; here restricted to Pompiere, Terre de Haut, Les Iles des Saintes.

*Diagnosis:* Dorsals in the standard distance 28 to 40 (average 33); 20 to 26 (average 25) subdigital lamellae; adult male grey-brown to green-brown, without dark speckles or vermicula-

tions; large blotches of bright yellow laterally and on nape fading to suffusions on posterior body and belly; yellow of orbital area often confluent with yellow blotching of nape and trunk; throat-fan yellow with yellow scales. Adult female grey-brown with a faint flank stripe briefly indicated and a striped or ladder middorsal pattern.

*Description:* An adult male from Pompiere, MCZ 70707, was pale brown-green, becoming browner on the head and blue-green on the tail. The orbital skin was ochre-yellow and suffused into the brown of the head. Virtually the entire costal region and lateral nape was blotched with three or four large areas of bright yellow pigment. There was no trace of dark marking. The throat fan was orange-yellow with yellow scales. The venter anteriorly was pale blue-green, almost lime-green, and faded to yellow in the abdominal region. Color change was merely to somewhat darker and browner. This specimen measured 76 mm snout to vent; a larger specimen, MCZ 70687, from Pointe Basse, Grande Ilet, measured 80 mm snout to vent and is the largest examined.

The adult female is pale grey-brown with a distinctly striped middorsal pattern. There is a short flank stripe, but it is not set off by darker borders above or below.

*Variation:* Throat fan color varies from butter-yellow to orange-yellow, and the scales vary from pale to bright yellow. Some specimens show rather heavy yellow pigmentation of the entire venter. Females vary little, and no geographic variation was noted in either sex among the several islands where this form occurs.

*Distribution: A. m. terraealtae* occurs throughout the low, dry area of Les Iles des Saintes; this includes Ilet-à-Cabrit, eastern Terre de Haut, Grande Ilet, and, presumably, La Coche. This area forms a crescent around the high, wetter, western end of the island of Terre de Haut and lies to the east of the also high, wetter island of Terre de Bas.

*Specimens examined:* MCZ 10628-30, "Terre d'en Haut" (Noble coll.); MCZ 70687-96, Pointe Basse, Grande Ilet; MCZ 70697-706, Ilet-à-Cabrit; MCZ 70707-17, Pompiere, Terre de Haut; MCZ 70718-22, Marigot, Terre de Haut.

*Discussion:* The type locality is restricted to Pompiere because the population on the western end of the island of Terre de Haut is intermediate between *terraealtae* and the form which occurs on Terre de Bas, *caryae*. Of fifteen specimens collected in the town of Terre de Haut (MCZ 70723-37), three (70730-32)

show definite *caryae* characteristics of both coloration and, to a slight extent, squamation. Several others of this series show an approach to *caryae* on squamation. An additional series, MCZ 70738-47, from Pointe-à-Cointe, Terre de Haut, are quite intermediate in squamation and vary considerably in color characters, approaching both *terraealtae* and *caryae*. The type series is severely discolored; on the basis of scale characters alone, however, they fit within the range of the form which occurs in the low, dry "crescent" of Les Saintes. These specimens probably were collected in the town of Terre de Haut, but on the basis of what can be discerned from them the name must, ironically, be applied to the form which occurs on the eastern end of the island of Terre de Haut. There is no precise locality data with them that could contradict restriction of the type locality to Pompiere. As in the case of the Pointe-des-Chateaux population between *inornatus* and *desiradei*, the population on western Terre de Haut is not of intergrades as such, but it is one which is both morphologically and geographically intermediate between two very different forms and not distinctive in its own right. The presence of this intermediate population necessitates classifying the last form to be described as:

ANOLIS MARMORATUS CARYAE subsp. nov.

*Holotype:* MCZ 70666, collected 6 September 1961 by J. D. Lazell, Jr.

*Type locality:* The town of Terre de Bas, Terre de Bas, Les Iles des Saintes.

*Diagnosis:* Dorsals in the standard distance 38 to 53 (average 47); 20 to 26 (average 23) subdigital lamellae; adult male pale green, becoming bright green posteriorly; a faint wash of yellow on abdomen, rest of belly lime green; fine vermiculations coalesce on the back of the head and the nape to produce a grey appearance; posteriorly these fine vermiculations produce distinct pale grey transverse markings; a pale, whitish flank stripe accentuated in the costal region by a lack of vermiculation; throat fan bright yellow with yellow scales; orbital area cream-colored. Adult female pale grey-green with ladder middorsal pattern and striking flank stripe set off by dark speckles above and below.

*Description of holotype:* This adult male was pale green with fine vermiculations so pronounced on the head, neck and anterior dorsum that the ground color appeared only as flecking

in this area. There was a sharp transition between this vermiculation and the grey transverse bands, though neither the vermiculations nor the bands were dark or bold compared to the green ground color. The flank stripe appeared as a continuation of the pale whitish chin and throat color and extended beyond the first transverse band. The throat fan was bright yellow with yellow scales, and the orbital skin was cream-colored. The dorsal scales are very small though not spinose. Color change was negligible. The holotype, 75 mm snout to vent, was the largest specimen examined.

*Variation:* The orbital skin may be pale yellow or cream-colored, probably depending more on the eye of the observer than anything else. Variation in this population is so slight with respect to the known sample that it defies description.

*Distribution:* This form is confined to Terre de Bas, Les Iles des Saintes.

*Paratypes:* MCZ 70667-76, same data as the type; MCZ 70677-86, Grande Anse, Terre de Bas, Les Iles des Saintes.

*Discussion:* That two such different anoles occur in the Saintes came as a complete surprise. When I discovered this fact I was struck by the similarity of *caryae* to *chrysops,* for I had not yet seen *desiradei.* In general, *caryae* bears a remarkable resemblance to a pale, faded *desiradei,* though there is, of course, an ample set of characters to unequivocally distinguish them. It is suggested that, aside from parts of the large and ecologically variable island of Marie Galante (see "Evolutionary Discussion"), the islands of Désirade and Terre de Bas are more ecologically similar than any of the other "satellite" islands: both are fairly high and rather homogeneously wetter than any other islands in the "satellite" group, including Marie Galante. The similarity between the anoles of Désirade and Terre de Bas, Les Saintes, is in my opinion the product of parallelism. There is no apparent resemblance between *caryae* and the anoles of La Guadeloupe except in those characters which define the species *marmoratus.* The relationships of *caryae* are obviously and directly to *terraealtae,* thence back through the stepped-cline series to *desiradei,* which is related to *inornatus* in the same manner as *caryae* is to *terraealtae.*

This form is named for Margaret M. Cary, who, in 1957, sponsored my first trip to the Caribbean; without her continuous inspiration and friendship since that time my life might have been a very different one, and I might never have seen the island of Terre de Bas.

## EVOLUTIONARY DISCUSSION

The fact that geographic variation within a single species has produced so many geographic units, herein described as subspecies, is remarkable. As I noted for *Anolis oculatus* on Dominica, ecological zonation appears to have produced this situation. On Dominica there are four subspecies: nominate *oculatus*, on the south coast, *winstoni*, on the wet, windward coast, *cabritensis*, on the dry, northern leeward coast, and *montanus*, in the central rain forest.

Dominica is the largest and highest of the first cycle islands on which an *Anolis* of the *bimaculatus* group occurs; though somewhat smaller in area, La Guadeloupe is closely similar in topographical conformation, and a comparison of these two islands is called for with respect to their *Anolis*.

Ecological zonation is produced, among the first cycle islands of the Lesser Antilles, by a combination of two factors: the predominant northeast wind and a range of high mountains. The predominant northeast wind may be considered as a vector in which the eastern component is the result of the inertia of the air mass surrounding the rotating earth, and the northern component is the result of convection currents produced by warmed air rising from the equatorial regions, cooling in the upper atmosphere, descending at the poles and pushing across the surface of the earth towards the equator. (In the Northern Hemisphere this amounts to a northerly wind direction.)

The mountain factor of this etiological combination is more complex. Cumulus, produced directly by evaporation off the tropical Atlantic, can be backed up on a chain of mountains, providing they are high enough and sufficiently close together, in such a way as to produce both a rain (or "cloud") forest zone through the mountains themselves, and a well-watered lowland region to windward. The result of this to leeward of the mountains is a lowland zone of low rainfall and generally arid conditions. In Dominica a chain of mountains that are demonstrably high enough and sufficiently close together to act as a moisture barrier begins, in the south, with Morne Anglais, and extends northward to the massif of Morne Diablotin. The mountains increase in height from south to north, in this case, and the result is a larger rain forest area, and a correspondingly more arid leeward coast area, at the northern end of the island. There is a broad gap between the Morne Diablotin massif, however, and the smaller, lower Morne Au Diable

massif at the north tip of the island. Morne Au Diable is, however, sufficiently high to back up cumulus of its own, and it also gets some rain from large amounts of cumulus backed up on Diablotin, at least during the rainy seasons of the year.

On La Guadeloupe a similar situation prevails: a series of peaks comparably high and continuous begins in the south with the Souffriere-Sans Toucher massif and continues northward to Morne Goton. There is not, however, a smaller, disjunct massif corresponding to Morne Au Diable in Dominica. Also, the highest montane area on La Guadeloupe is at the southern end: the Souffriere-Sans Toucher massif produces the largest rain forest area, and, correspondingly, the most arid region is the southern leeward coast. La Guadeloupe, then, has the ecological zonation of Dominica, but in mirror image.

On Dominica, the Morne Au Diable massif is well watered but never attains genuine rain forest conditions even at its highest points. The result of this is a large area at the north tip of Dominica that is a sort of "ecological mongrel." Rain forest, as such, does not appear, but the country is decidedly wetter at lower elevations than elsewhere on the island. This area contains an anole that is morphologically intermediate between a coastal form (*winstoni*) and the montane form (*montanus*), and this intermediate occurs at much lower elevations at the northern end of the island than do intergrades with *montanus* elsewhere.

On La Guadeloupe, where the Souffriere-Sans Toucher massif is at the south end, very close to the tip of the island, and there is no disjunct massif closer to the coast, the "ecologically mongrel" area is at the southern tip. It is therefore suggested that the presence of *alliaceus* influence at sea level, combined with coastal *girafus* influence, at the south tip of La Guadeloupe is directly the product of ecological conditions.

It may be noted, however, that in Dominica the tip-population anole is intermediate between the montane and *wet, windward coast* forms; on La Guadeloupe the tip-population is intermediate between the montane and *dry, leeward coast* forms.

*Anolis oculatus montanus*, of Dominica, is an entirely green anole with a dark throat fan and white, black-bordered, lateral spots. *Anolis marmoratus alliaceus*, of La Guadeloupe, is an entirely green anole with a dark throat fan and black, light-bordered, spots. The convergence is obvious, but I am unable to account for a selection pressure which would produce such spot-patterns.

Similarly, *Anolis oculatus cabritensis,* from the arid coast of Dominica, has a striped pattern composed of coalescing light spots on a darker ground color. *Anolis marmoratus girafus,* from the arid coast of La Guadeloupe, has pale, coalescing spot series. In this case the convergence seems to result from a selection pressure operating to produce "outline-breaking" color patterns in forms which occupy the sparsely vegetated scrub-thornbush areas of both islands. Similar "outline-breaking" patterns appear in most of the other dry country forms. There is also a correspondence between Dominica and La Guadeloupe dry country forms with respect to their clinality. In both cases a bright color begins at each end of the range and fades out clinally towards the middle.

A geographical convergence may be noted between the south coast form of *A. oculatus* (nominate *oculatus*), on Dominica, and the north coast form of *A. marmoratus* (*sctosus*), on La Guadeloupe, but no morphological convergence is readily apparent.

La Guadeloupe has, in reality, two wet, windward coast forms: nominate *marmoratus* and *speciosus.* Southwestern Grande Terre is ecologically confluent with the "waist" between Grande Terre and La Guadeloupe (which is part of La Guadeloupe), and there is no reproductive break between *speciosus* on either side of the narrow estuary which separates them. In fact, though I never stopped to collect them, anoles were seen on the bridge across this estuary, Rivière Saline. There is no apparent morphological convergence between either of the La Guadeloupe windward coast forms and *winstoni* of Dominica.

The second cycle islands of the Lesser Antilles are generally dry. An exception is southwestern Grande Terre, which is close enough to the mountains of La Guadeloupe to be well-watered lowland. In the Guadeloupéen archipelago, two of the second cycle islands, La Désirade and Marie Galante, are high enough to get at least more rain than does northeastern Grande Terre or Les Iles de la Petite Terre. Désirade rises abruptly to elevations of nearly 300 m, and is rather high throughout. Marie Galante, on the other hand, is rather "lumpy" in topography, like southwestern Grande Terre, but neither high enough (*ca.* 200 m at the highest point) to collect much rain of its own nor adjacent to a mountain range that could back up rain-bearing clouds over it.

The results of the above conditions are that Désirade is fairly homogeneous in ecological conditions and wetter than northeastern Grande Terre. Marie Galante, however, is ecologically

diverse, but the diversity is not in the form of geographical zones: dry country and rather lush, wet country alternate in patches all over Marie Galante. It is suggested that this complex situation with respect to ecology may account for the extreme variability of *A. m. ferreus* on Marie Galante.

Further, a generalization suggests itself: wide-ranging dry country anoles are more variable than wet country anoles. This generalization would obviously not hold in cases like Les Iles de la Petite Terre and the low, dry "crescent" of Les Saintes because in these very small geographic areas the ecological conditions are fairly homogeneous. In the larger, generally dry areas, however, there are always ravines, ponds, or coastal marshes that provide patches of more or less lush vegetation, and thus ecological diversity, within the encompassing "dry country" region. If variability is a function of ecological diversity, then this generalization is valid.

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## SUMMARY

A collection of 792 *Anolis* from 77 localities on 13 islands of the Guadeloupéen archipelago is reported on. The islands include La Guadeloupe ("Basse-Terre"), Grande Terre, La Désirade, Marie Galante, Ilet-à-Kahouanne, Ilet-à-Fajou, Ilet-à-Cochons (ou Gouvernement), both of Les Iles de La Petite Terre, and four of Les Iles des Saintes. Five previously named populations are reviewed and redefined: *marmoratus*, *alliaceus*, *ferreus*, *speciosus*, and *terraealtae*. Seven previously undescribed populations are described and named: *girafus*, *setosus*, *kahouannensis*, *inornatus*, *desiradei*, *chrysops*, and *caryae*. All twelve populations are regarded as subspecies of *Anolis marmoratus* Duméril

and Bibron, 1837. The concept of Simpson's (1961) "evolutionary species" is utilized and discussed; criteria for determining continuity of evolutionary role among insular populations are enumerated. The role of ecological zonation in subspeciation is discussed relative to *Anolis marmoratus* and other species of the *bimaculatus* group.

## SOMMAIRE

Une collection de 792 *Anolis* de 77 localités de treize îles de l'archipel Guadeloupéen est décrite. Les îles comprennent La Guadeloupe ("Basse Terre"), Grande Terre, La Désirade, Marie Galante, Ilet-à-Kahouanne, Ilet-à-Fajou, Ilet-à-Cochons (ou Gouvernement), les deux Iles de la Petite Terre, et quatre des Iles des Saintes. Cinq populations, précédemment nommées, sont revues et redéfinies: *marmoratus, alliaceus, ferreus, speciosus*, et *terraealtae*. Sept populations non-décrites auparavant sont décrites et nommées: *girafus, setosus, kahouannensis, inornatus, desiradei, chrysops*, et *caryae*. Les douze populations sont toutes considérées comme sous-espèces d'*Anolis marmoratus* Duméril et Bibron, 1837. La notion de "l'espèce evolutive" de Simpson (1961) est adoptée et discutée; Les critères pour la définition de la continuité du rôle evolutif de ces populations insulaires sont définis. Le rôle de la zonation écologique dans la formation des sous-espèces est considéré chez *Anolis marmoratus* et d'autres espèces du groupe *bimaculatus*.

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TABLE 1

Some color characteristics of adult males of the twelve subspecies of *Anolis marmoratus* in the Guadeloupéen archipelago.

| Subspecies | Ground Color | Markings | Throat Fan Skin | Throat Fan Scales | Orbital Area |
|---|---|---|---|---|---|
| *marmoratus* | green + blue | orange marbling anteriorly | orange-yellow | yellow | marbled orange |
| *alliaceus* | green | light bordered, dark spots | dull orange | green | brown-green lids white |
| *girafus* | brown to green + blue | light reticulations setting off dark areas | yellow | white | brown |
| *setosus* | green + blue | dark, temporary, transverse bars | yellow | greenish | dark green |
| *kahouannensis* | chartreuse (= bright yellow-green) | none | yellow | yellow | greenish |
| *speciosus* | green + blue | none | yellow | greenish | sky blue |
| *inornatus* | dull greenish | faint transverse bars; flank stripe | yellow | white | brown |
| *desiradei* | pale grey-green | vermiculations | yellow | white | red |
| *chrysops* | pale grey-green | vermiculations reduced | yellow | yellow | red-gold |
| *ferreus* | grey-brown + green | flecking | yellow ± grey | yellow ± grey | dull-yellow |
| *terraealtae* | grey-brown + green | yellow blotches | yellow | yellow | dull-yellow |
| *caryae* | pale green | fine, pale vermiculations | yellow | yellow | cream-colored |